VEGETATION, SOIL, AND FLOODING RELATIONSHIPS IN A BLACKWATER FLOODPLAIN FOREST

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Abstract: Hydroperiod is considered the primary determinant of plant species distribution in temperate floodplain forests, but most studies have focused on alluvial (sediment-laden) river systems. Few studies have evaluated plant community relationships in blackwater river systems of the South Atlantic Coastal Plain of North America. In this study, we characterized the soils, hydroperiod, and vegetation communities and evaluated relationships between the physical and chemical environment and plant community structure on the floodplain of the Coosawhatchie River, a blackwater river in South Carolina, USA. The soils were similar to previous descriptions of blackwater floodplain soils but had greater soil N and P availability, substantially greater clay content, and lower soil silt content than was previously reported for other blackwater river floodplains. Results of a cluster analysis showed there were five forest communities on the site, and both short-term (4 years) and long-term (50 years) flooding records documented a flooding gradient: water tupelo community > swamp tupelo > laurel oak = overcup oak > mixed oak. The long-term hydrologic record showed that the floodplain has flooded less frequently from 1994 to present than in previous decades. Detrended correspondence analysis of environmental and relative basal area values showed that 27% of the variation in overstory community structure could be explained by the first two axes; however, fitting the species distributions to the DCA axes using Gaussian regression explained 67% of the variation. Axes were correlated with elevation (flooding intensity) and soil characteristics related to rooting volume and cation nutrient availability. Our study suggests that flooding is the major factor affecting community structure, but soil characteristics also may be factors in community structure in blackwater systems.

Key Words: bottomland hardwoods, classification, ordination, wetland, hydroperiod

INTRODUCTION

Timing, depth, and duration of flooding are considered the primary determinants of plant species composition in temperate floodplain forests (Wharton et al. 1982, Kellison et al. 1998, Mitsch and Gosselink 2000), although a few studies have shown that soil texture can be a factor (Robertson et al. 1978, 1984) and that soil fertility is associated with differences between floodplain and adjacent upland communities (Gemborys 1974). Seldom has soil fertility been correlated with community composition within floodplain forests (Parsons and Ware 1982).

To date, most studies of floodplain forests in the United States have been conducted in alluvial rivers that differ geomorphically, hydrologically, and chemically from blackwater river systems (Hupp 2000). In contrast to alluvial rivers, blackwater rivers are low-gradient rivers that arise on the Coastal Plain and have

lower sediment loads, pH, hardness, and specific conductance than alluvial rivers. Because blackwater river watersheds are small, hydroperiods are characterized by short duration floods that may be deep and widespread, followed by extensive periods of lower discharge. Blackwater river flow often is not sustained, and extended droughts during the growing season occur in these floodplains (Wharton et al. 1982). As a result, soil characteristics, such as water-holding capacity, nutrient availability, and rooting volume, may be more important in structuring blackwater floodplain plant communities than those in more alluvial systems. There have been few detailed studies of soil characteristics in blackwater systems (Stanturf and Schoenholtz 1998) and none that explore the potential influence of physical, chemical, and biological soil characteristics on vegetation composition.

The objectives of this study were to characterize the vegetation, soils, and hydroperiod in a blackwater river floodplain and to evaluate the major factors associated with tree species distribution. Admittedly, the use of only one site in this study constitutes pseudoreplication, but alternative study sites were limited due to massive conversion of these formerly abundant ecosystems. Of the few other forested blackwater river floodplains that remain, major changes in hydroperiod and land use makes them not useful for this type of study. The Coosawhatchie River floodplain was relatively undisturbed and can be considered representative of blackwater floodplain forests along the South Atlantic Coast Plain.

METHODS

Study Area

The study area is a 350-ha tract owned by MeadWestvaco Corporation in Jasper County, South Carolina, United States (32° 40′N and 80° 55′W), just above tidal influence on the Coosawhatchie River (Figure 1). The river is a fourth order, anastamosing, blackwater stream that drains a 1,012-km^2 watershed in southeastern South Carolina (Abrahamsen 1999). Through erosion and down cutting, the river carved a fluvial valley through the Wicomico and Pamlico marine terraces during the late Pleistocene-Holocene. Today, the floodplain is relatively small and immature compared to the major river systems of the South Carolina Lower Coastal Plain, so the classic geomorphic features of larger rivers are subtly expressed (Murray et al. 2000). The Coosawhatchie River floodplain is representative of the formerly numerous blackwater river floodplains in the Atlantic Coastal Plain, which were extensively cleared and drained for agriculture (Mitsch and Gosselink 2000) or intensively logged, or

high graded by removal of the largest and best trees, leaving stands with low stocking and poor quality species composition (Hodges 1998). Although the Coosawhatchie River floodplain was not cleared and drained for agriculture, logging and probably high-grading has occurred in the past. Dominant trees on the site are 80+ years old (John Martin, Mead-Westvaco Corporation, personal communication), and evidence of the most recent logging on the site (stumps and remnants of railway roads) dates to before 1950. The naturally regenerated bottomland hardwood forest grades into upland mixed hardwood-pine forest and loblolly pine plantations.

The study site has two weakly developed terraces, distinguished primarily by flooding frequency and surface sand size. Soils of the lower terrace consist of highly variable loamy and clayey Pamlico and recent fluvial sediments over older sandy fluvial beds and have been mapped mainly in the Brookman series, a fine mixed thermic Typic Umbraqualf. In much of the floodplain, there is a confining layer of clay in soil depths between 30 and 100 cm (Murray et al. 2000). The less scoured soils in the floodplain are mapped in the Meggett series, a fine, mixed, thermic Typic Albaqualf. Approximately 20 percent of the lower terrace was in the Okeetee, Coosaw, Elloree, Grifton, Osier, and Rutledge series where calcareous marine sediments underlie the surface soil. The higher, second terrace is mapped in the Nakina soil series, a fine-loamy, siliceous thermic Typic Umbraqualf.

Relief on the study site is approximately 2 m and is characterized by distinct microtopography of convex hummocks and scoured swales with sandy channel bars and small natural levees (Murray et al. 2000). The hydroperiod is relatively unaltered, as the river has not been channelized, and dams and levees are not present on the river (Eisenbies and Hughes 2000). The dominant land uses in the watershed are agriculture (42 percent), forestry (30 percent), and wetlands (24 percent) (Maluk et al. 2000).

Floods on this site are typical of blackwater rivers in that they are of relatively short duration, floodwaters may be deep and widespread, and floods are followed by extensive periods of low discharge. Ground-water recharge was the dominant hydrologic condition on the site, but discharge occurred during extremely low flows in the summer (Eisenbies and Hughes 2000).

Field and Laboratory Procedures

In fall 1994, we established three transects perpendicular to the prevailing elevation gradient. A total of 66 rectangular (6.0 m × 66.6 m) sampling plots (Robertson et al. 1978, Dollar 1992) were established, with the long axes of the plots aligned with the elevation

contours. This design minimized the environmental variability within plots and maximized the variability among plots. No plots were established within 50 m of any non-natural edge (e.g., power lines, roads). Elevations at the centers of each plot were determined using standard surveying techniques.

Species and diameter of each tree ($\geq$ 5.0 cm diameter) were recorded. Many trees were buttressed; thus, diameter of all trees was measured at 2 m above ground level to provide a constant measuring height. Basal area, relative basal area, density, relative density, and importance values (relative density + relative basal area) were calculated for each tree species in each plot. Botanical nomenclature followed Radford et al. (1968).

Soil samples were collected from the A- and B-horizons at representative points outside the four corners of each sampling plot. After removing the forest litter layer, the first 15 cm of the A-horizon (if available) was collected with a push probe. A bucket soil auger was then used to determine the depth to the B-horizon, and a sample of the B-horizon was taken. Four subsamples were composited by horizon for the plot sample. These soil samples were air-dried in paper bags and then ground to pass through a 2-mm sieve. The samples were analyzed at Waters Laboratory in Camilla, Georgia for pH, soil organic matter (Walkley and Black 1934), and for the entire suite of ICP (inductively coupled plasma emission spectrometer) elements after double acid extraction (Soltanpour et al. 1982). Soil texture was analyzed by the hydrometer method (Day 1965) at the Center for Forested Wetlands Research, Charleston, South Carolina.

Once the major vegetation types were identified (see below), a subsample of plots from each designated vegetation type was randomly chosen for further study, including estimating the plant-availability of nitrogen on the four major communities (those comprising 10% or more of the area of the site). *In situ* soil incubations were conducted at three randomly chosen points in the designated communities. On June 6, July 7, August 8, September 9, and October 10, 1997, 200 g of soil was collected from the surface 15 cm of soil below the forest floor and was thoroughly mixed. One-half of each sample was incubated *in situ* within sealed plastic bags for 30 days, at which time it was processed as described below. The other half of the fresh sample was processed immediately. Processing included extracting the fresh soil with 2 M KCl within 48 h as in Burke et al. (1992) and analyzing for nitrate using a technicon autoanalyzer I and for ammonium using a Wescan ammonium analyzer at Walters Laboratory.

A detailed characterization of the hydroperiod was made for the four major communities, those comprising more than 10% of the area on the study site. From October 1994 to October 1998, river stage height was measured on the site and from July 1996 to October 1998, water-table elevations were measured manually every two weeks in 18 pvc wells. Also during this latter interval, water levels of the surficial aquifer were recorded continuously in four wells installed adjacent to and in the river channel. Individual regressions of water-table elevations on the site were produced using as independent variables the river stage and continuously recording wells and as dependent variables the manually measured water-level elevations. The best regressions were used to model water levels in the four major communities during the four years during which stage height data was collected and during the previous 50-year intervals as described below.

The percent of time flooded and the time saturated to a depth of 30 cm was calculated for both entire years and for growing seasons, assumed to be March 15 to September 30. The best equations (best correlation between independent and dependent variables) were used to estimate percent of time flooded or saturated at 30-cm soil depths, for the four-year interval and for the 50-year interval. Because the only long-term data available were from the Hampton Branch Station, 24 km upstream from the site, that site was used in estimating hydroperiod on the site for the 50-year interval. The threshold discharge from the Hampton Branch Station that would result in flooding or saturation of soil at a 30-cm depth was estimated for each plot that contained a well. These threshold values were used to calculate the percentage of days each plot was flooded or saturated, and means for each community type were determined. Because the river crested on the site three to four days after cresting at the Hampton Branch Station (Eisenbies and Hughes 2000), the equations produced offset the crest on the site by three days.

Data Analyses

Standard cluster analysis was performed on importance values (sum of relative basal area and relative density for overstory component) using SAS PROC CLUSTER (SAS 1987). The procedure is an agglomerative classification technique that uses information on all species. Each sample was assigned to a cluster with a single member and then the cluster agglomerated in a hierarchy of progressively larger clusters until a single cluster contained all the samples. Ward's (1963) minimum-variance method was used to define the distance between clusters. To reduce the number of dimensions, species with < 1% of the basal area were dropped, then the cluster analysis was repeated. The plots were broken into clusters at an average distance of 0.9 (90% of the information was remaining).

The validity of the clusters was analyzed with the multi-response permutation procedure (Biondini et al. 1985). Each community was named based on the trees with the greatest relative basal area.

Indicator species analysis (Dufrêne and Legendre 1997) in PC-ORD software (McCune and Mefford 1997) was used to test for statistical significance (p ≤ 0.05) of indicators using a Monte Carlo technique. This analysis employed the concentration of species abundance within communities identified by cluster analysis and the faithfulness of occurrence for each species within those communities.

Linear correlations among soil properties and elevation, an index of hydroperiod, were estimated using Pearson correlation analysis procedure of SAS. Soil nitrogen was not used in either the correlation or ordination analyses because nitrogen was not estimated for each plot. To test for differences in soil and microsite variables among plant communities, the soil and microsite variables were first analyzed using Bartlett's homogeneity of variance test (Steele and Torrie 1960), analysis of variance (ANOVA), and Scheffe's mean separation technique (SAS PROC GLM; SAS Version 6, 1987). Variables that failed Bartlett's test, indicating heterogeneity of variance, were transformed according to Kirk (1982:84) and reanalyzed. Variables that failed Bartlett's test after being transformed were analyzed using generalized least squares (Searle 1971).

We used a variety of ordination techniques for indirect gradient analysis, including non-metric multidimensional scaling (McCune and Mefford 1997), detrended canonical correspondence analysis (CANOCO; ter Braak 1987–1992), and detrended correspondence analysis (DCA; CANOCO; ter Braak 1987–1992), to evaluate the major environmental factors associated with the overstory stratum of the communities. Similar results were obtained for all three techniques, and we report only those obtained with DCA.

Because of the large amount of co-linearity among the environmental variables, some of the less ecologically important variables that had high correlation with other environmental variables were dropped from the DCA analysis (i.e., aluminum, magnesium, molybdenum, lead, strontium, and H-ion concentration in the A horizon, and aluminum, calcium, magnesium, molybdenum, lead, strontium, H-ion concentration, and cation exchange capacity for the B horizon) to ease explaining the results (ter Braak 1987–1992). Subsequently, the environmental factors were tested for correlation with the first two DCA ordination axes to evaluate relationships between environmental factors and plant community structure along the axes. Correlation coefficients were restricted to a Bonferroni significance level of ≤ 0.05.

The ratio of the eigenvalues of the ordination axes to the total inertia is usually used to determine the amount of variation in vegetation composition explained by the environmental variables. However, Oklund (1999) showed that this statistic underestimates the amount of variation explained, so we also calculated the amount of variation explained after fitting the importance values to the ordination axes via Gaussian regression as in Robertson et al. (1984). The percent of variation explained was calculated using the sum-squared error and the total sums of squares corrected for the individual species means. The 50-year hydrology data sets were summarized using Duncans Multiple Range tests in mean separation of the arcsine of percent of time flooded and saturated at a depth of 30 cm.

RESULTS

There were 30 tree species documented in the analysis. Tree density was 919 trees ha^{-1} ± 33.8 (mean ± 1 SE.), and basal area was 46 m^2 ha^{-1} ± 1.5. Cluster analysis (Figure 2) indicated five distinguishable plant associations: (1) water tupelo (*Nyssa aquatica* L.) stands contained > 30% water tupelo, (2) swamp tupelo (*Nyssa sylvatica* var. *biflora* (Walter) Sargent) stands contained > 9% of the basal area (but usually > 25%) in water tupelo, swamp tupelo, and bald cypress (*Taxodium distichum* (L.) Richard) and < 15% in laurel oak, (3) overcup oak (*Quercus lyrata* Walter) stands had > 25% of the basal area in overcup oak, 4) laurel oak (*Quercus laurifolia* Michaux) had > 15% (but usually more) of the basal area in laurel oak, and (5) mixed oak had > 30% of the basal area in willow oak (*Q. phellos* L.), water oak (*Q. nigra* L.)., and cherrybark oak (*Q. pagodifolia* Raf.). The multi-response permutation procedure *t*-value test statistic for the five communities was 18.4 (p < 0.001).

Water tupelo was a significant indicator of the water tupelo community, swamp tupelo for the swamp tupelo community, overcup oak and water hickory (*Carya aquatica* (Michaux f.) Nuttall) for the overcup oak community, laurel oak for the laurel oak community, and magnolia (*Magnolia grandiflora* L.), cherrybark oak, willow oak, water oak, blackgum, yellow poplar (*Liriodendron tulipifera* L.), red bay (*Persea borbonia* (L.) Sprengel), and spruce pine (*Pinus glabra* Walter) for the mixed oak community. Because the overcup oak community comprised only 6% of the study plots, detailed characterizations of hydrology and nitrogen mineralization were not performed for that community.

Elevation on the study site ranged from 3.8 m to 5.8 m above mean sea level. The river level fluctuated more than 1.5 m between October 1994 and October 1998, floods occurred throughout each year, and both

Table 1. Mean percent of time flooded above the soil surface and saturated above 30 cm soil depths for th four main communities during the growing season (March 15–October 1) for the four years of intensive measurements and for the 50-year record. Different superscripts indicate significant differences from other communities for that year.

	Growing Season (May 15–Sept. 30)	Mixed Oak	Laurel Oak	Swamp Tupelo	Water Tupelo
% of time flooded above soil surface	1994	2.4[a]	14.8[b]	47.1[c]	54.1[c]
	1995	1.5[a]	13.8[b]	36.3[c]	51.7[c]
	1996	0[a]	5.2[b]	19.5[c]	27.2[c]
	1997	5.2[a]	33.6[b]	40.7[b]	45.5[b]
% of time saturated at 30 cm soil depth	1994	23.3[a]	47.4[b]	68.2[c]	78.4[c]
	1995	16.4[a]	41.2[b]	66.3[c]	80.7[c]
	1996	14.6[a]	20.8[a]	54.0[b]	72.3[b]
	1997	27.9[a]	40.9[ab]	54.2[bc]	69.7[c]
% of time flooded (for 50 year record)	minimum	7	8	25	30
	1st quartile	12	29	53	72
	median	18	36	69	82
	mean	19	38	68	79
	3rd quartile	25	50	82	91
	maximum	46	80	99	99

floods and periods of very low flow occurred during the growing season. Water-table elevations for the four main plant communities measured in the wells were strongly correlated with all seven continuous recording stations. Correlation coefficients ranged between 0.56 and 0.97, but all well locations had at least one available station with a correlation coefficient greater than 0.85. The water levels in wells closest to the river correlated best with the river stage. The Hampton gauge was able to predict the absolute water-table elevation, with a correlation coefficient greater than 0.75 on all plots with wells except those in the mixed oak plots. Since the data are summarized over the course of the whole year as the percent of time above and below the flooded threshold, these r-square values are satisfactory.

The four main communities had distinct hydrologic regimes during both the 50-year and the four-year analysis periods, although there were year-to-year variations (Tables 1–4). Consistently, sites could be ranked from wettest to driest using both percent flooding and percent saturation measures: water tupelo > swamp tupelo > laurel oak > mixed oak, although differences between some community types were not significant in the arcsine of the percent of time flooded nor percent of time saturated within a 30 cm soil depth. Several specific trends should be noted among the four intensively measured years. Between 1994 and 1997, 1) there were no differences in percent of time flooded between the swamp tupelo and water tupelo communities, but there were differences ($\alpha \leq 0.05$) in percent of time flooded among the mixed oak, laurel oak, and tupelo communities; 2) in three of the four years during the growing season, there were differences be-

tween the laurel oak and swamp tupelo sites; 3) in most years, the mixed oak sites were drier than the other community types; and 4) percent of time flooded was 10 to 25% greater when comparisons were made for the water year relative to the growing season. The 50-year record showed consistent trends in the duration of flooding among communities, although recent years had shorter flood durations than previous years. Because elevations for overcup oak were similar to those of the laurel oak community, hydroperiods on overcup oak sites could be estimated by referring to the laurel oak sites.

Soil differences among communities (Tables 5–6) were more pronounced in the A- than B-horizon for soil organic matter, percent clay, percent sand, CEC and Ca and Mg availability. Differences were more pronounced in the B- than the A-horizon for P and aluminum availability. In addition, elevation, depth to B-horizon, Munsel chroma, and bulk density and porosity in both horizons differed among plant communities.

The overcup oak community had relatively high pH, percent base saturation, and bulk density, and had relatively low organic matter content, cation exchange capacity (CEC), and porosity. Water tupelo and swamp tupelo communities had relatively high CEC, available nutrient cations, organic matter, clay content, porosity in both horizons, and low depth to the B-horizon, sand content, and bulk density in both horizons. Mixed oak sites had relatively low percent base saturation in both horizons, pH in the A horizon, percent clay in both horizons, and relatively high P availability in the B-horizon. Nitrogen availability was similar among the communities in both initial and min-

Table 2. Summary of analysis of variance for hydroperiod during growing seasons (March 15–Sept. 30) 1994–1997.

Source		1994					1995					1996					1997			
	df	MS	F	p	R^2	df	MS	F	p	R^2	df	MS	F	p	R^2	df	MS	F	p	R^2
% of time flooded at soil surface																				
Community	6	0.339	19.2	0.0001	0.928	6	0.338	10.75	0.0011	0.878	6	0.236	9.71	0.0017	0.866	6	0.216	12.55	0.0006	0.893
error	9	0.018				9	0.031				9	0.024				9	0.017			
% of time saturated at 30 cm soil depth																				
Community	6	0.189	13.29	0.0005	0.898	6	0.259	16.39	0.0002	0.916	6	0.286	9.76	0.0016	0.867	6	0.098	7.66	0.0039	0.836
error	9	0.014				9	0.016				9	0.029				9	0.013			

eralized soil nitrogen. The laurel oak community tended to be intermediate in many respects but had shallow depth to B-horizon and high bulk density in the B-horizon.

Soil variables that were positively correlated with elevation were depth to the B horizon (r = 0.55), P in the B horizon (r = 0.53), Na in the A horizon (r = 0.46), and sand in the A horizon (r = 0.45) and B horizons (r = 0.38). Soil values that were negatively correlated with elevation were clay in the A (r = −0.42) and B (r = −0.36) horizons and organic matter in the B horizon (r = −0.36). Also associated with elevation was greater depth to saturation, reduction in bulk density in the B-horizon, and greater Munsel chroma values. These soil characteristics, combined with the decreasing frequency and depth of flooding with increasing elevation, suggested that rooting volume (the amount of soil roots can penetrate) increased up the elevation gradient. As a result, mid-elevation had the greatest probability of both flood and drought occurring on the same site.

The amount of variation explained by the first two ordination axes, 27%, was based on the traditional ratio of eigenvalues-to-total-inertia method estimated. In contrast, 67% of the variation was explained when Gaussian curves were fitted to the ordination axes. The DCA axis 1 and 2 scores for each sample plots are graphed in Figure 3, with plots designated by community as was previously described. DCA1 was highly positively correlated (based on Bonferroni p < 0.05 |r| >0.39), with elevation (r^2 = 0.81), sand content in the A-horizon (r^2 = 0.46), and depth to the B-horizon (r^2 = 0.40), and was negatively correlated with organic matter in the B-horizon (r^2 = −0.53), clay content in the A-horizon (r^2 = −0.44), Ca availability in the A-horizon (r^2 = −0.44), and K availability in the B-horizon (r^2 = −0.43). DCA2 was negatively correlated with pH (A-horizon: r^2 = 0.62; B-horizon: r^2 = 0.42) and percent base saturation (A-horizon: r^2 = −0.64; B-horizon: r^2 = −0.62). Community separation appeared most closely related to flood frequency, factors associated with rooting volume, and cation nutrient availability (Figure 4).

DISCUSSION

Vegetation groups were characterized successfully using cluster and indicator species analyses that resulted in statistically significant indicator species for which the clusters of plots could be named. These analyses relied solely on measures of species abundance and faithfulness of occurrence, without consideration of the environmental factors associated with the communities. Because plant species vary independently along environmental gradients, and there were

Table 3. Mean percent of time flooded above the soil surface and saturated above 30 cm soil depths for the four main communities during water years (October 1 to September 30) for the four years of intensive measurements, and for the 50 year record. Different superscripts indicate significant differences from other communities for that year.

	Water Year (Oct. 1–Sept. 30)	Mixed Oak	Laurel Oak	Swamp Tupelo	Water Tupelo
% of time flooded above soil surface	1994	7.7[a]	45.4[b]	70.7[c]	74.6[c]
	1995	0.8[a]	16.3[b]	60.6[c]	66.3[c]
	1996	0[a]	13.2[b]	37.3[c]	42.2[c]
	1997	11.7[a]	47.2[b]	60.4[bc]	63.4[c]
% of time saturated above 30 cm soil depth	1994	53.4[a]	70.8[b]	82.5[bc]	88.1[c]
	1995	28.2[a]	66.3[b]	81.5[b]	89.4[b]
	1996	27.7[a]	35.2[a]	67.2[b]	82.0[b]
	1997	46.6[a]	60.4[b]	71.2[bc]	81.7[c]
% of time flooded (for 50 years of record)	minimum	8	8	45	55
	1st quartile	14	29	67	79
	median	21	36	74	84
	mean	22	38	73	83
	3rd quartile	28	50	81	90
	maximum	44	80	96	93

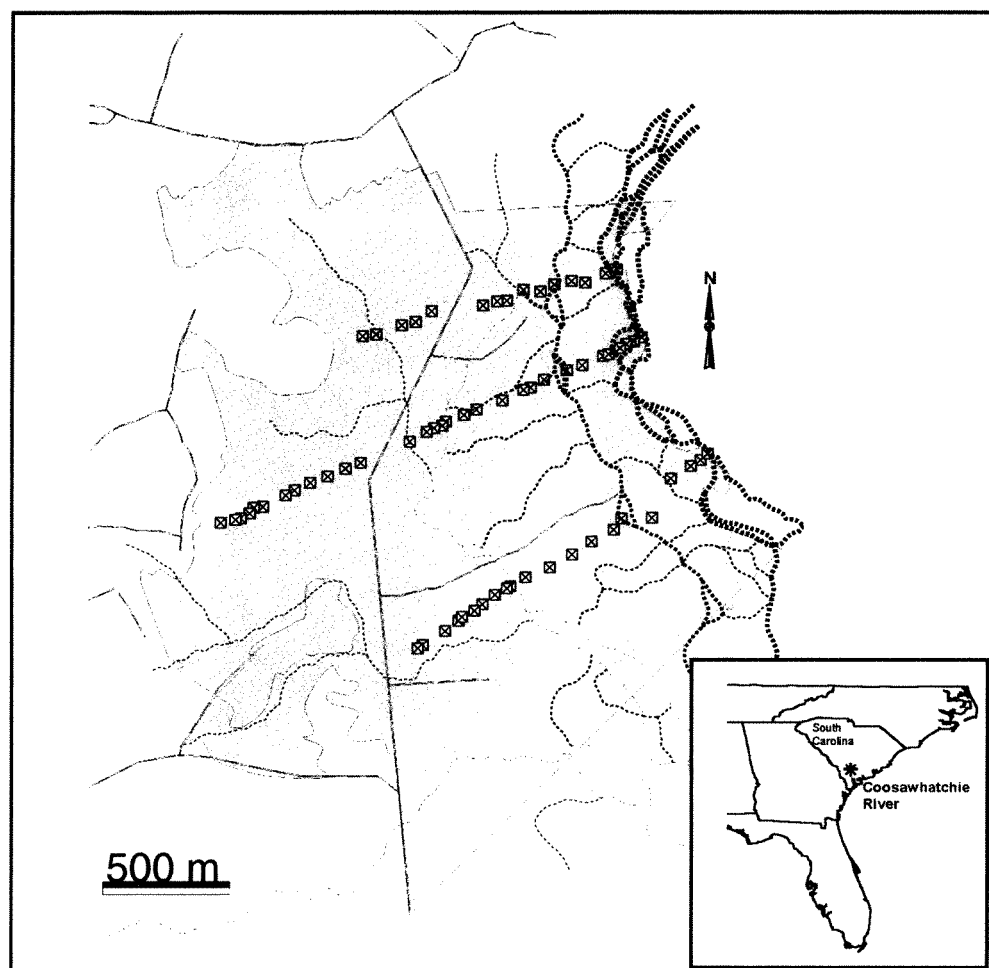Note: means separations were based on the arcsine of the percent.

Figure 1. Site map of the Coosawhatchie Bottomland Ecosystem Study showing the location of the ordination plots along three transects, roads (══), main river channels (▪▪▪▪), primary sloughs (▪▪▪▪▪), secondary sloughs (_ _ _ _), and connecting sloughs (· · · ·). The insert is the locator map.

Table 4. Summary of analysis of variance for hydroperiod during water years (Oct. 1–Sept. 30) 1994–1997.

Source		1994				1995				1996				1997			
	df	MS	F	p	R^2	df	MS	F	p	R^2	df	MS	F	p	R^2	df	MS	F	p	R^2

	Source	df	MS	F	p	R^2	df	MS	F	p	R^2	df	MS	F	p	R^2	df	MS	F	p	R^2
% of time flooded at soil surface — Community	6	0.372	50.37	0.0001	0.971	6	0.587	18.16	0.0001	0.924	6	0.392	12.56	0.0006	0.893	6	0.228	24.72	0.0001	0.943
error	9	0.007				9	0.032				9	0.031				9	0.009			
% of time saturated at 30 cm soil depth — Community	6	0.059	8.78	0.0024	0.854	6	0.235	9.5	0.0018	0.864	6	0.201	8.01	0.0033	0.842	6	0.057	10.13	0.0014	0.871
error	9	0.007				9	0.025				9	0.025				9	0.006			
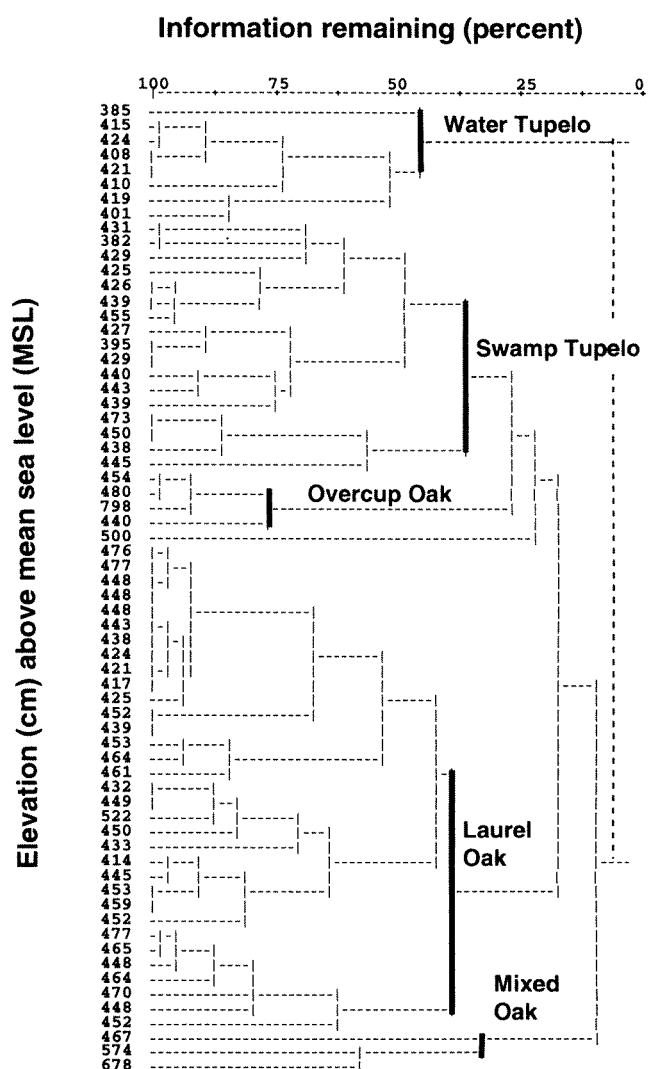
Figure 2. Dendrogram produced using cluster analysis on importance values for each plot.

complex environmental gradients on this site, it is not surprising that there was substantial overlap of plots assigned to different communities when they were plotted along the first two DCA axes (Figure 3). Nevertheless, we were successful in identifying the factors correlated with variation in community structure and in quantifying the percent of variation they explained.

Our results suggest that flooding intensity, as well as soil physical and chemical characteristics, can affect tree species distributions in blackwater river forests. Although most previous studies of alluvial systems have indicated that elevation is a major factor affecting plant species distributions (Larson et al. 1981, Wharton et al. 1982, Sharitz and Mitsch 1993), our data suggest that soil characteristics also may influence the structure of vegetation communities in blackwater systems. Floodplains of alluvial rivers in larger watersheds have younger, deeper, more fertile and porous

Table 5. Mean (standard error) soil characteristics in the five plant communities[5]

		Water Tupelo	Swamp Tupelo	Overcup Oak	Laurel Oak	Mixed Oak
CEC: A[1]	meq/100 g	2458.4 (378.9)[abc]	2081.6 (230.7)[ab]	1000.3 (146.0)[cd]	1516.6 (90.5)[abcd]	1366.6 (68.3)[acd]
CEC: B[1]	meq/100 g	2327.1 (433.2)[a]	1778.7 (219.3)[a]	962.3 (46.4)[b]	1166.2 (44.2)[a]	1292.1 (370.4)[a]
Base saturation: A	(%)	25.2 (4.2)	21.3 (4.1)	39.6 (2.2)	24.4 (2.6)	4.9 (0.8)
Base saturation: B	(%)	31.7 (5.4)	27.3 (5.0)	49.6 (4.2)	40.7 (3.8)	13.2 (6.9)
pH: A		4.6 (0.1)	4.4 (0.1)	4.9 (0)	4.5 (0)	4.3 (0.1)
pH: B		4.7 (0.1)	4.5 (0)	4.9 (0.1)	4.6 (0)	4.7 (0.1)
Aluminum: A[1]	ppm	1478.9 (274.0)[a]	1230.6 (196.1)[a]	405.7 (99.2)[b]	788.7 (73.5)[a]	680.5 (85.2)[a]
Aluminum: B[2]	ppm	1338.4 (327.6)[abc]	1011.1 (209.4)[abc]	295.5 (31.6)[a]	404.2 (45.5)[b]	884.3 (367.9)[c]
Barium: A[1]	ppm	1.2 (0.4)[A]	3.0 (0.7)[AB]	3.4 (0.6)[B]	3.5 (0.6)[B]	5.0 (0.6)[B]
Barium: B[1]	ppm	1.0 (0.3)[A]	2.8 (0.7)[B]	3.3 (0.3)[B]	2.9 (0.5)[B]	4.1 (0.7)[B]
Calcium: A[3]	ppm	829.4 (175.2)[ab]	460.2 (75.2)[ab]	581.6 (87.8)[c]	492.2 (52.3)[ab]	78.2 (18.6)[bc]
Calcium: B[3]	ppm	971.4 (0.8)[bc]	533.2 (87.2)[bc]	645.7 (147.8)[c]	734.4 (69.6)[c]	111.5 (45.4)[a]
Chromium: A	ppm	0.4 (0.7)	0.6 (0.1)	0.3 (0.0)	0.6 (0.1)	0.4 (0.1)
Chromium: B	ppm	0.4 (0.8)	0.6 (0.1)	0.6 (0.1)	0.6 (0.1)	1.0 (0.4)
Cobalt: A	ppm	0.4 (0)	0.4 (0)	0.3 (0)	0.3 (0)	0.2 (0)
Cobalt: B	ppm	0.3 (0.5)	0.3 (0)	0.2 (0)	0.3 (0)	0.2 (0)
Copper: A	ppm	0.7 (0.1)[a]	1.2 (0.2)[ab]	2.4 (0.3)[b]	1.4 (0.2)[ab]	1.3 (0.5)[ab]
Copper: B	ppm	0.9 (0)	1.2 (0.2)	1.9 (0.2)	1.0 (0.1)	1.1 (0.3)
Iron: A	ppm	143.6 (24.3)	132.2 (24.8)	83.1 (4.4)	157.1 (14.8)	144.1 (28.5)
Iron: B[1]	ppm	191.1 (28.5)[A]	191.6 (38.6)[AB]	84.7 (7.5)[B]	176.8 (14.3)[A]	129.8 (25.7)[AB]
Lead: A[4]	ppm	3.8 (0.7)[a]	3.6 (0.4)[abc]	1.6 (0.2)[c]	2.8 (0.3)[ab]	2.5 (0.4)[b]
Lead: B[4]	ppm	3.4 (0.8)[a]	2.8 (0.5)[b]	0.8 (0.1)[c]	1.3 (0.1)[c]	2.4 (1.0)[abc]
Magnesium: A	ppm	165.5 (28.4)[A]	105.6 (11.5)[A]	87.5 (19.9)[AB]	97.6 (8.6)[A]	25.9 (3.2)[B]
Magnesium: B	ppm	162.1 (26.4)	102.6 (10.1)	115.2 (12.6)	104.0 (8.8)	60.6 (25.1)
Molybdenum: A	ppm	0.4 (0)[A]	0.4 (0.1)[AB]	0.2 (0)[AB]	0.2 (0.00)[B]	0.2 (0)[AB]
Molybdenum: B	ppm	0.4 (0)[A]	0.3 (0)[AB]	0.2 (0)[AB]	0.2 (0)[B]	0.3 (0.1)[AB]
Nickel: A	ppm	0.6 (0.7)	0.6 (0.1)	0.5 (0.1)	0.5 (0)	0.4 (0)
Nickel: B[4]	ppm	0.8 (0.8)	0.7 (0.1)	0.6 (0.1)	0.7 (0.1)	0.7 (0.2)
Nitrogen (initial)[6]	mg/kg soil	39.7 (10.3)	33.6 (5.7)	n.d.	39.9 (1.6)	25.5 (4.1)
Nitrogen (mineralized)[7]	mg/kg soil	8.6 (8.6)	9.4 (5.2)	n.d.	15.6 (4.7)	24.6 (8.4)
Phosphorus A	ppm	52.4 (9.9)	48.0 (6.6)	31.9 (7.0)	32.1 (3.1)	44.0 (12.8)
Phosphorus B[4]	ppm	39.4 (14.6)[A]	25.6 (6.1)[AB]	10.0 (2.1)[AB]	9.4 (1.7)[B]	120.3 (75.5)[AB]
Potassium: A	ppm	44.7 (6.4)	38.2 (4.8)	33.6 (2.4)	33.0 (2.4)	24.3 (2.7)
Potassium: B	ppm	35.0 (6.5)	22.6 (1.3)	24.6 (4.6)	21.0 (0.5)	20.6 (0.6)
Silicon: A[1]	ppm	29.0 (5.5)[A]	30.8 (7.7)[A]	13.0 (6.2)[AB]	17.3 (2.0)[A]	4.9 (0.9)[B]
Silcon: B	ppm	44.4 (8.6)	33.9 (4.2)	19.9 (4.5)	31.8 (2.8)	45.7 (24.2)
Sodium: A[1]	ppm	28.9 (3.9)[A]	26.4 (1.4)[A]	18.7 (4.1)[AB]	23.7 (1.7)[A]	7.8 (0.7)[B]
Sodium: B[1]	ppm	35.4 (4.0)[A]	40.1 (9.5)[AB]	27.4 (2.0)[A]	49.2 (5.4)[B]	11.7 (2.9)[C]
Strontium: A[4]	ppm	4.7 (0.9)[A]	3.0 (0.4)[A]	2.5 (0.7)[AB]	3.0 (0.3)[A]	0.7 (0.2)[B]
Strontium: B[2]	ppm	5.5 (0.8)[A]	3.5 (0.5)[A]	3.7 (0.9)[AB]	4.3 (0.3)[A]	0.8 (0.3)[B]
Zinc: A	ppm	3.6 (0.4)	5.0 (0.9)	3.4 (0.3)	3.4 (0.2)	3.5 (0.7)
Zinc: B	ppm	3.5 (0.6)	3.2 (0.5)	2.4 (0.4)	2.0 (0.2)	4.0 (1.8)

Table 5. Continued.

		Water Tupelo	Swamp Tupelo	Overcup Oak	Laurel Oak	Mixed Oak
Organic Matter: A	(%)	8.1 (1.2)[AB]	7.8 (0.8)[A]	4.6 (0.5)[B]	5.6 (0.3)[AB]	5.0 (0.4)[B]
Organic Matter: B	(%)	6.0 (1.3)	4.1 (0.7)	2.8 (1.0)	2.0 (0.2)	1.1 (0.3)
Elevation above sea level	m	4.2 (0)[A]	4.3 (0)[AB]	4.6 (0.1)[ABC]	4.5 (0)[BC]	5.7 (0.4)[C]
Depth to B	cm	24.4 (3.9)[A]	28.2 (4.6)[A]	52.3 (13.3)[AB]	30.8 (3.1)[A]	60.8 (5.5)[B]
Clay: A[3]	(%)	37.2 (4.5)[A]	29.4 (2.6)[C]	13.9 (5.6)[B]	24.4 (1.4)[BC]	14.6 (1.5)[BC]
Clay: B[1]	(%)	42.8 (5.9)[AB]	41.2 (2.5)[A]	36.3 (2.2)[AB]	32.6 (1.4)[B]	25.7 (3.1)[B]
Sand: A[1]	(%)	49.7 (5.9)[A]	60.3 (3.2)[A]	81.8 (4.6)[BC]	66.3 (2.1)[AB]	82.7 (1.)[C]
Sand: B[1]	(%)	44.1 (7.1)[AB]	48.6 (3.9)[A]	62.6 (4.7)[AB]	57.2 (2.0)[A]	68.3 (3.6)[B]
Munsel Chroma		2.2 (0.1)[A]	2.3 (0.1)[A]	2.3 (0.2)[AB]	2.2 (0.1)[A]	3.1 (0.3)[B]
Munsel Value		0.3 (0.1)	0.7 (0.3)	0.8 (0.2)	0.8 (0.2)	1.1 (0.3)
Bulk Density: A[1]	g/cm^{3}	0.8 (0.6)[A]	1.0 (0.1)[AB]	1.3 (0.1)[B]	1.1 (0)[B]	1.2 (0.1)[B]
Bulk Density: B[1]	g/cm^{3}	1.0 (0.1)[A]	1.2 (0)[A]	1.6 (0.1)[B]	1.4 (0)[B]	1.5 (0)[B]
Porosity: A[1]	(%)	0.7 (0.2)[A]	0.6 (0)[AB]	0.5 (0)[B]	0.6 (0)[B]	0.5 (0)[B]
Porosity: B[1]	(%)	0.6 (0.4)[A]	0.6 (0)[A]	0.4 (0)[B]	0.5 (0)[B]	0.4 (01)[B]

[1] Transformed using General Least Squares.
[2] Transformed using Log transformation.
[3] Transformed using the square root transformation.
[4] Transformed using reciprocal transformation.
[5] Values within rows followed by the same upper case letter are not significantly (p = 0.05) different and values within rows followed by the same lower case letter are not significantly (p = 0.1) different.
[6] Mean total KCl extractable N (NH$_4$+ NO$_3^-$) in fresh soil collected on June 6, July 7, August 8, September 9, and October 10, 1997.
[7] Mean total KCl extractable N in fresh soil after 1 month of in situ incubation in samples collected and incubated beginning on June 6, July 7, August 8, September 9, and October 10, 1997.

Table 6. Summary of analysis of variance for (significant) environmental variables.

Soil Variable	Source	df	MS	F	p	R^2
CEC: A[1]	Community	4	5.38	5.38	0.0009	0.264
	Error	6	1.0			
CEC: B[1]	Community	4	7.21	7.22	0.0001	0.325
	Error	60	1.00			
Aluminum: A[1]	Community	4	6.408	6.41	0.0001	0.296
(ppm)	Error	61	1.00			
Aluminum: B[2]	Community	4	658	3.39	0.014	0.184
(ppm)	Error	60	194			
Barium: A[1]	Community	4	8.9	8.91	0.001	0.369
(ppm)	Error	61	1.00	9.49		
Barium: B[1]	Community	4	9.492	9.49	0.0001	0.384
(ppm)	Error	61	1.00			
Calcium: A[3]	Community	4	658	3.39	0.0145	0.185
(ppm)	Error	60	194.2			
Calcium: B[3]	Community	4	658	3.39	0.0145	0.185
(ppm)	Error	60	194.2			
Copper: A	Community	4	2.172	3.01	0.025	0.167
(ppm)	Error	60	0.721			
Iron: B[1]	Community	4	11.533	11.53	0.0001	0.435
(ppm)	Error	60	1.00			
Lead: A[4]	Community	4	0.002	3.78	0.008	0.201
(ppm)	Error	60	0.006			
Lead: B[4]	Community	4	0.087	5.2	0.0012	0.257
(ppm)	Error	60	0.017			
Magnesium: A	Community	4	30.577	30.58	0.0001	0.667
(ppm)	Error	61	1.00			
Molybdenum: A	Community	4	0.109	4.16	0.0048	0.2144
(ppm)	Error	61	0.026			
Molybdenum: B	Community	4	0.086	3.79	0.0081	0.199
(ppm)	Error	1	0.022			
Phosphorus B[4]	Community	4	0.0228	3.90	0.0070	0.206
(ppm)	Error	60	0.006			
Silicon: A[1]	Community	4	14.230	14.23	0.0001	0.483
(ppm)	Error	61	1.00			
Sodium: A[1]	Community	4	53.334	53.33	0.0001	0.778
(ppm)	Error	61	1			
Sodium: B[1]	Community	4	12.642	12.64	0.001	0.457
(ppm)	Error	60	1.000			
Strontium: A[4]	Community	4	0.1334	6.93	0.0001	0.312
(ppm)	Error	61	0.0192			
Strontium: B[2]	Community	4	0.0676	6.60	0.0002	0.302
(ppm)	Error	61	0.0102			
Organic Matter: A	Community	4	4.664	4.66	0.0024	0.2342
(ppm)	Error	61	1.0			
Elevation above	Community	4	9.408	9.41	0.0001	0.385
Sea level (m)	Error	60	1			
Depth to B horizon	Community	4	1660.6	5.77	0.0005	0.274
(cm)	Error	61	288.0			
Clay: A[3]	Community	4	7.087	7.96	0.0001	0.343
(%)	Error	61	0.890			
Clay: B[1]	Community	4	4.952	4.95	0.0016	0.248
(%)	Error	60	1.00			
Sand: A[1]	Community	4	27.217	27.22	0.0001	0.641
(%)	Error	61	1			
Sand: B[1]	Community	4	4.618	4.62	0.002	0.232
(%)	Error	61	1			
Munsel Chroma	Community	4	0.904	5.37	0.0009	0.260

Table 6. Continued.

Soil Variable	Source	df	MS	F	p	R[2]
	Error	61	0.168			
Bulk Density: A[1]	Community	4	0.283	7.06	0.0001	0.327
(g/cm³)	Error	58	0.040			
Bulk Density: B[1]	Community	4	13.45	13.45	0.0001	0.481
(g/cm³)	Error	58	1.0			
Porosity: A[1]	Community	4	0.0403	7.06	0.0001	0.327
(%)	Error	58	0.0057			
Porosity: B[1]	Community	4	13.450	13.45	0.0001	0.481
(%)	Error	58	1.000			

[1] Transformed using General Least Squares.
[2] Transformed using Log transformation.
[3] Transformed using the square root transformation.
[4] Transformed using reciprocal transformation.

soils, with a lower probability of moisture deficit (Wharton et al. 1982, Lockaby and Walbridge 1998). In contrast, soils in blackwater river floodplains tend to be older and shallower than soils along rivers carrying higher sediment loads (Hupp 2000). Because watersheds are small, extremes in soil moisture are more likely than in the larger floodplains of alluvial rivers. In the more flood-prone communities on our site (i.e., water tupelo, swamp tupelo), consistently high moisture and nutrient availability probably mitigated potential effects of shallow rooting depth. In consistently flooded sites, flood stress limits tree species to only the most flood tolerant. On the dry end of the gradient in the mixed oak community, lower soil bulk density, greater soil porosity, and less frequent flooding allows deeper rooting and, thus, greater access to nutrients and low susceptibility to drought. In contrast, soils in

the laurel oak community allow only shallow rooting due to high bulk densities and low soil porosities in the B-horizons that impede drainage and root penetration. Also, frequent flooding can limit rooting depth.

The volume of soil available for root growth likely influences plant community structure because it influences nutrient availability (Pritchett 1979, Brady 1984) and susceptibility to drought (Kozlowski 1997) between flooding episodes. Rooting depth appears to be limited at the lower elevations of this site (Burke and Chambers 2003). As a result, distributions of tree species are probably influenced by species differences in flood and drought tolerance and the ability to obtain nutrients from a limited rooting depth.

Much has been published on flood tolerance in trees (e.g., Kozlowski 1997, McKevlin et al. 1998), but little has been published on other life history strategies for floodplain tree species. Changing water-table levels can result in greater root mortality (Burke and Cham-
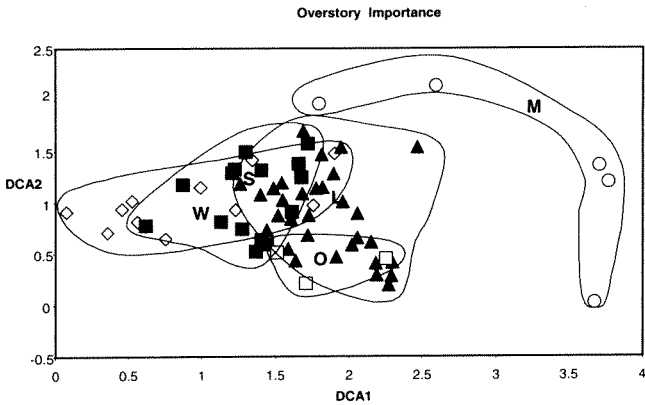

Figure 3. Ordination of tree species importance values and DCA 1 and DCA 2 scores for each ordination plot. Community designations are those determined for each plot in the cluster analysis: mixed oak (○), laurel oak (▲), overcup oak (□), swamp tupelo (■), water tupelo (◇). The ordination space occupied by each community is encircled, and the mean axis score of each community is represented by the initials of that community.
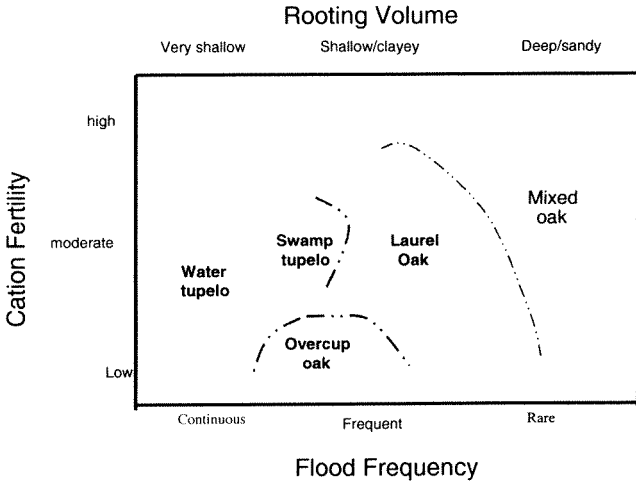

Figure 4. Proposed relationships among site characteristics and forest communities on the Coosawhatchie Bottomland Ecosystem Study site.

bers 2003), may predispose trees to drought stress (Pritchett 1979), and are associated with greater energy requirements for trees compared to sites with less extreme variations in soil moisture (Crawford 1993). Tree species that are successful in the more intermediate elevations on this site seem to avoid these stresses by timing growth to seasons when potential flood or drought stresses are least likely. For example, overcup oak inhabits poorly drained soils in the first bottoms of the lower coastal plain (Solomon 1990) and avoids flood stress through an abbreviated growing season; seasonal root and leaf growth occurs later in the spring than for other oak species (Burke and Chambers 2003). This stress avoidance strategy is advantageous on wet but nutrient-poor sites that exclude flood-intolerant and more competitive species. However, because this species produces fewer roots than other tree species (Burke and Chambers 2003), overcup oak is probably a poor competitor on better sites; trees that produce more roots are more effective in acquiring moisture and nutrients (Kramer 1983, Fitter and Hay 1987).

Laurel oak dominates the flats of the floodplains of all major rivers in the southeastern U.S. (Wharton et al. 1982). This species is tolerant of short-term flooding, extended droughts, and restricted rooting depths (McReynolds and Hebb 1990). Part of its success in these habitats may be due to its semi-evergreen life history strategy, a characteristic of trees in subtropical areas that have pronounced dry seasons (Pearcy and Robichaux 1985). In habitats with variable moisture availability, semi-evergreen plants can avoid droughts and assimilate carbon dioxide throughout the year when conditions are favorable, an advantage not shared by neighboring deciduous trees (Waring 1991). In fact, laurel oak appeared to be quite successful on the Coosawhatchie site; both above- and belowground net primary productivity were relatively high in that community (Burke et al. 2000b).

Our detailed vegetation, soil, and flooding relationships in the Coosawhatchie River floodplain were generally consistent with previously published descriptions of blackwater floodplains rivers (Wharton et al. 1982, Stanturf and Schoenholz 1998): soils were acidic and had high per cent soil organic matter. Also, the Coosawhatchie River had low sedimentation rates (Hupp and Schening 2000), and flood events were numerous but relatively short in duration (Eisenbies and Hughes 2000). These floodplain soils had substantially greater clay and sand content, lower silt content, tended to be more acidic, and had higher soil N and P availabilities than had been previously described for blackwater river floodplains. In fact, these results support the suggestion by Lockaby and Walbridge (1998)

that the Coosawhatchie River floodplain is relatively fertile.

Our study also provides insights to the hydrology of blackwater floodplain systems. The hydroperiod is variable both within and among years in this floodplain. As a result, short-term studies have a potential of underestimating the wetland area; based on date from October 1994 to September 1998, the mixed oak community probably would not be considered a jurisdictional wetland, although the longer-term analysis showed that community has a high probability of flooding during the growing season. This retrospective showed that 1994–1998 were some of the driest years in the 50-year record, although subsequent years (1998–2002) were even drier (unpublished data).

We should note that the hydrologic data from this site also suggest that municipal and industrial water use can impact wetlands. Ground-water withdrawal by Beaufort, South Carolina and Savannah, Georgia, within 60 km of the study site, appears responsible for a 5-m decrease in the potentiometric surface of the Floridian aquifer during the last century (Hughes et al. 1989). Our record of a drying trend on the site hydrologic record may reflect this decrease in the potentiometric surface in the reduced ground- and surface-water flow. Ultimately, this change can influence vegetation community dynamics through long-term shifts from wetter to drier species compositions. This study provides a baseline for monitoring the impacts of water use on floodplain resources in the region.

In summary, the results of this study support previously published descriptions of floodplain forests (Larson et al. 1981, Wharton et al. 1982, Sharitz and Mitsch 1993) in that elevation is highly correlated with plant species distribution. However, our results also indicate that rooting volume and nutrient availability may be important in structuring communities. Additional studies are needed to determine whether these relationships are consistent across other blackwater river systems or whether they are unique to the Coosawhatchie River floodplain.

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